Fossil fruit of the Macadamieae (Proteaceae) in the Tertiary of eastern Australia: *Eureka* gen. nov.

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ABSTRACT

Eureka gen. nov. is proposed to accommodate fossil fruits recovered from several mid-Tertiary (early Oligocene-Miocene) sites in eastern Australia. The type (*E. welcomensis* sp. nov.) and other described species (*E.*(*al. Conchotheca*) *turgida* (F. Muell.) comb. nov., *E. spechtii* sp. nov., *E. harslettiae* sp. nov.) have bilaterally symmetrical, ellipsoidal pericarps that are uniloculate, 1-seeded, and tardily dehiscent along the ventral suture and dorsal hinge line. The pericarp wall is radially structured and has a branched vasculature system capped by fibres embedded in a thick mesocarp; the radial fibres extend into the exocarp, and the endocarp is thin or lacking. The seed is orthotropous, attached apically and with a 2-layered seed coat that has an endotestal cuticle bearing impressions of transfer cells. *Eureka* is morphologically and anatomically consistent with fruits of extant members of *Bleasdalea* F. Muell., *Hicksbeachia* F. Muell., and *Gevuina* Molina of subtribe Gevuininae (tribe Macadamieae, family Proteaceae). Accordingly, the fossil fruit evidence implies that the Gevuininae had a former distribution range spanning some 20° of latitude in eastern Australia and taken together with fossil cuticle evidence a trans-Tasman distribution no longer mirrored in the present vegetation. *Eureka* also displays some resemblance to the tardily dehiscent fruits of extant *Panopsis* (subtribe Macadamiinae, tribe Macadamieae); however, morphological/anatomical details of extant members are imprecisely known. ☐ *Australia, Bleasdalea, Eureka, fossil fruit, Gevuina, Hicksbeachia, Macadamieae, Tertiary.*

Among recently recovered woody fossils from Tertiary sediments at several localities in Queensland are several different types of 1-seeded, tardily dehiscent, uniloculate fruits with vascularised pericarps similar to those of fruits borne by several extant genera included within tribe Macadamieae (Proteaceae) as recently redefined (Weston & Barker 2006; Mast et al. 2008). The Queensland fossil fruits are spheroidal to ellipsoidal, near-symmetrical about the vertical axis, and their thick pericarp has a distinctive radial structure reflecting a branched vasculature system embedded in a thick, woody mesocarp. Similarly structured pericarps characterise fruits borne by extant genera of tribe Macadamieae. The distinctive vasculature pattern with 'third-order radial vascular bundles' (Johnson & Briggs 1975, p.134; Douglas 1995, p.18) comprises prolific radial branching of the main vertical and lateral (tangentially-aligned) bundles in a woody ground mass of predominantly radially oriented fibre sheaths that surround the bundles as detailed for fruits of several extant members of the tribe (Filla 1926; Strohschen 1986a,b). The Queensland fossil fruits with their near vertical symmetry,

near-smooth outer surface of pericarp, and one apically attached unwinged seed having a 2-layered, non-woody seed coat are more similar to fruits of several genera (*Gevuina* Molina, *Hicksbeachia* F. Muell., and *Bleasdalea* F. Muell.) of subtribe Gevuininae than to other members of tribe Macadamieae. Previously described fossil fruits that possess a thick pericarp with third order vasculature were assigned to *Conchotheca turgida* F. Muell., a taxon reported from mid-Tertiary deep lead sediments in Victoria (Mueller 1874a, Deane 1925) and Tasmania (Johnston 1880). Mueller (1874a) did not comment on the botanical affinity of *C. turgida*, but examination of his protocol material confirms these fossils, too, are morphologically consonant with fruits of subtribe Gevuininae, being similar to those of *Gevuina*, *Bleasdalea*, and *Hicksbeachia*. Evaluation of Mueller's protocol material and of the Queensland fossil fruits form the basis of the present study. Moreover, comparisons have been undertaken of the fossil material with fruits of extant *Gevuina*, *Hicksbeachia*, and *Bleasdalea*.

Extant *Gevuina* is monotypic and endemic to southern South America; *Bleasdalea* has two species, one each in New Guinea and eastern Australia, and *Hicksbeachia*, with two species, is endemic to eastern Australia (Fig 1A; Weston & Barker 2006). Fossil cuticles that are consistent with those of subtribe Gevuininae have been reported from Eocene sediments of Western Australia (Carpenter & Pole 1995) and from the Miocene of New Zealand (Pole 1998). Fossil wood similar to, but not identical with, *Gevuina* has been reported from the Oligocene of Patagonia (Pujana 2007).

The fossil pollen taxa, *Propylipollis reticuloscabratus* (Harris) Harris and Martin, and *P. tripartus* Harris, which occur in Campanian-Tertiary sediments of Australia, New Zealand and Antarctica, are morphologically similar to pollen of *Gevuina*, *Bleasdalea*, and *Hicksbeachia* (Martin 1982; Dettmann & Jarzen 1990, 1996, 1998). *P. reticuloscabratus* however, has been

shown to be insufficiently discriminatory of the extant taxa in parsimony analyses (Sauquet et al. 2009); thus far, *P. tripartus* has not been tested in any comparable cladistic analysis.

MATERIAL

Fruits reported upon here include woody and charcoalified and permineralised specimens. The charcoalified specimens were recovered from subsurface sediments near Blackwater and Moranbah, central Queensland and Bundaberg, southeastern Queensland and the permineralised specimens are from an outcrop at Glencoe, central Queensland; all are held in the Queensland Museum (QMF). Also examined are woody and charcoalified fruits collected in the late 1800's and early 1900's from several goldfield sites in Victoria and New South Wales and housed in the Queensland Museum, the Australian Museum (AMF) and the Museum of Victoria (NMVP). The last-mentioned collection contains the type and other specimens of the protocol material of *Conchotheca turgida* F. Muell.,1874, which was originally housed in the Museum of the Geological Survey of Victoria (GSVF). Locality details of occurrences of *Eureka* gen. nov. are as follows (see also Fig. 1B).

Queensland. a) Picardy Station, near Moranbah (21°5'17.6'S 147°50'34.3'E) Rio Tinto Exploration Hole RDPD98MA21, sands, silts and lignites at 123-133 m; Early Oligocene (Dettmann & Clifford 2001).

b) Near Blackwater (24°1'1.3'S 148°48'50'E) South Blackwater Coal Pty Ltd Hole R8736, sands and lignites at 82m; Early-Late Oligocene (Dettmann & Clifford 2001).

c) Glencoe Station (23°36'S 148°06'E), near Capella, silcrete outcrop; Oligocene-?Early Miocene (Rozefelds 1990; Rozefelds & Christophel 1996; Dettmann & Clifford 2001).

d) N of Bundaberg (24° 46'49'S 152°18'17'E), Herberts on Welcome Creek Drain, subsurface

sands and clays; Early Miocene (Dettmann & Clifford, 2003).

e) Near Clifton (27° 55'S 151° 55'E), Queensland Water Resources borehole, sands and lignites at 45-46 m; Tertiary (?Miocene).

New South Wales. Near Orange (33° 17'S 149° 06'E, Forest Reefs Mine, deep lead sediments; late Middle-early Late Miocene (Johnson 1989; Dettmann & Clifford 2001)

Victoria. a) Nintingabool (Crucible Co. Shaft), near Haddon (37° 18'S 146°32'E), SW of Ballarat, deep lead sediments; Oligocene-Miocene (Greenwood et al. 2000; Dettmann & Clifford 2001; Holdgate et al. 2006).

b) Foster (37° 10'S 146°14'E), deep lead sediments; Oligocene-Miocene (Rozefelds & Christophel 1996; Holdgate et al. 2008).

Tasmania. Brandy Creek, Beaconsfield (41° 12'S 148°49'E), deep lead sediments; Oligocene (Forsyth 1989)

METHODS

Fruits studied include carbonaceous specimens retaining well preserved morphological and anatomical characters of their woody tissues to severely vitrinised specimens retaining external and internal morphology but with few anatomical characters preserved. Some of the carbonaceous fruits are pyritised and, as a result of oxidation since collection, several have fragmented. Permineralised specimens are composed of amorphous and/or cryptocrystalline quartz that has preserved external and internal morphology of the fruits, but no anatomical detail of the original tissues is preserved.

Charcoalified specimens were photographed either after whitening with ammonium chloride to highlight surface features or without whitening to illustrate internal characters including those of the locules, seeds, and internal anatomy. Permineralised specimens were photographed without whitening. Thin sections of charcoalified specimens were cut using a slide microtome and mounted in glycerine jelly on glass slides for transmitted light microscope analysis. Fragments of several specimens were mounted on stubs and gold plated for scanning electron microscope analysis. Anatomical features of seed coats were examined in transmitted light after clearing in a weak solution of sodium hypochlorite, followed by thorough washing in distilled water.

Photographs were captured on either T Max film or digitally using an Olympus Cameida C-5050 camera. Images were processed using Photoshop 5LE.

SYSTEMATIC DESCRIPTION

FAMILY - PROTEACEAE JUSS.

SUBFAMILY - GREVILLEOIDEAE ENGL.

TRIBE - MACADAMIEAE C.VENKATA RAO

SUBTRIBE - GEVUININAE L.A.S. JOHNSON & B.G. BRIGGS

Genus -*Eureka* gen.nov.

Derivation of name. With reference to the association of 'Eureka' (Eureka Stockade, Eureka Flag, Eureka Deep Lead) with early gold mining activities in and around Ballarat, Victoria.

Generic diagnosis. Fruit unilocular, indehiscent to tardily dehiscent woody follicle; ellipsoidal or spheroidal, symmetrical about the vertical axis. Style base near-opposite stalk in the vertical plane; ventral suture and dorsal hinge line approximately equal in length; splitting along ventral suture and dorsal hinge into 2 near equal portions. Surface smooth or near-smooth. Pericarp largely composed of meso-carp, the outer thicker part with a branched vascular system composed of vertically aligned
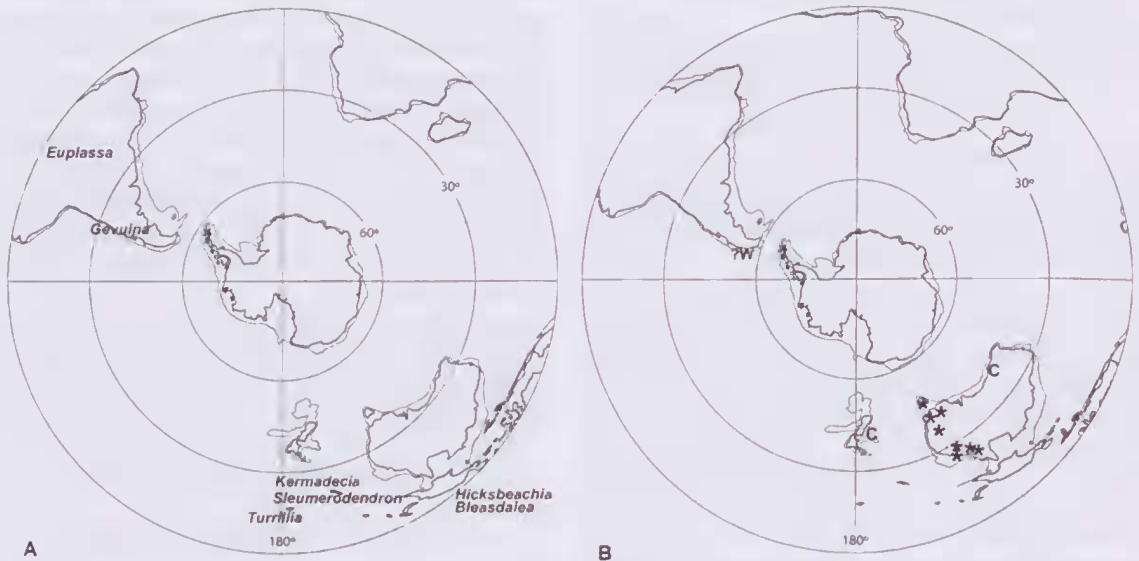
FIG. 1. Polar stereographic projections, based on Lawver & Gahagan (2003). A, Present Day showing distribution-range of extant members of Subtribe Gevuininae (excluding *Cardwellia*); B, Early Miocene (20 Mya) showing localities of fossil *Eureka* (*), fossil cuticles (C) of Subtribe Gevuininae, and fossil wood (W) questionably allied to Subtribe Gevuininae.

(tangential) primary bundles from which branch radially aligned secondary bundles that are surrounded by tangentially and radially aligned fibre bundles; fibres interspersed with parenchyma. Exocarp and endocarp thin. Seed solitary, unwinged, orthotropous, attached apically, filling, or almost so, locule. Seed coat 2-layered, the outer layer incompletely enveloping the inner; outer layer a cuticle with impressions of transfer cells; inner layer a cuticle with anticlinal walls of rectilinear cells.
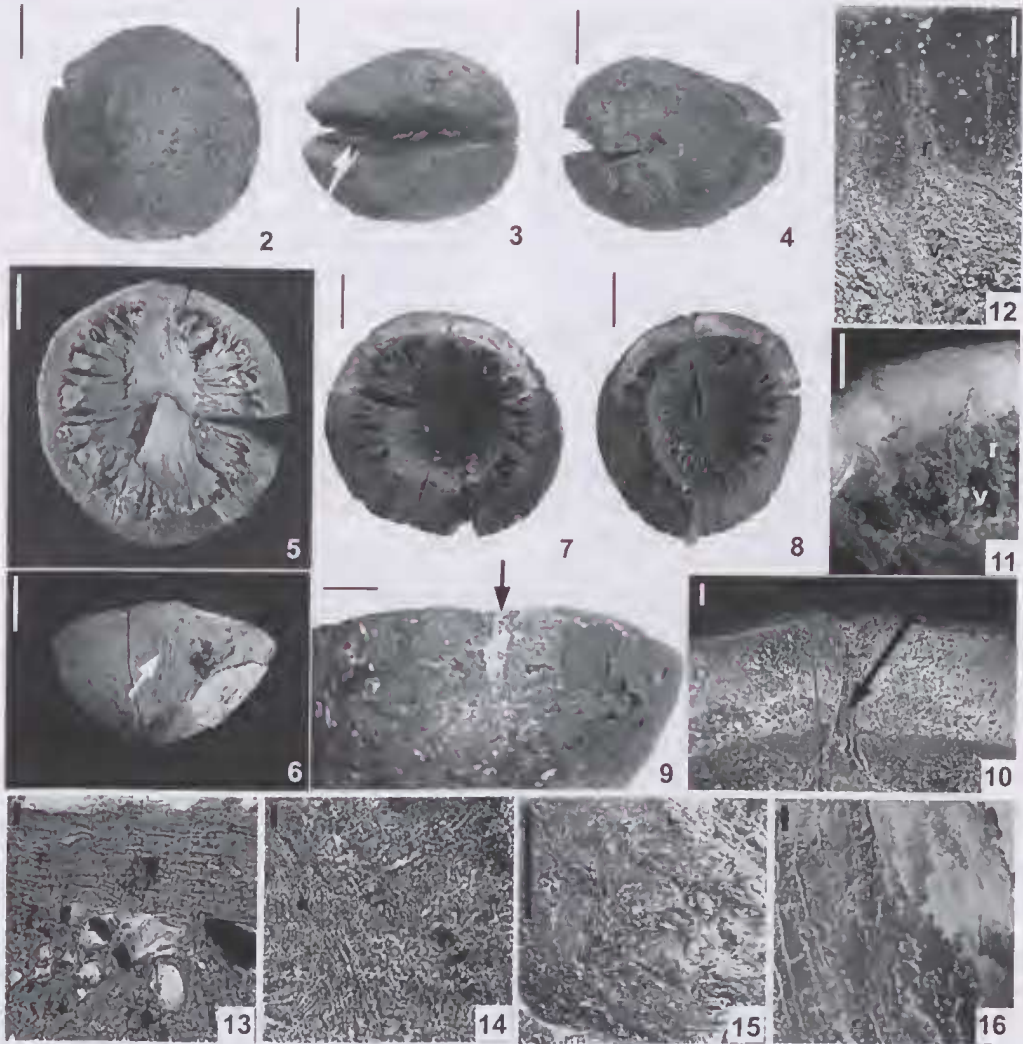
Type species. *Eureka welcomensis* sp. nov.

Remarks and comparison. *Eureka* gen.nov. accommodates uniloculate fruits having a branched vascular system surrounded by fibre bundles in the mesocarp, and a single apically attached, orthotropous seed. In these respects *Eureka* differs from *Conchotheca* F. Muell., emend. Dettmann & Clifford 2005, which includes fruits having vertically aligned, unbranched vascular bundles in the mesocarp and laterally attached seeds. One taxon, *C. turgida*, allocated to *Conchotheca* by Mueller (1874a) is characterised by a pericarp with a branched vascular system and an apically attached, orthotropous seed; this species is transferred herein to *Eureka*.

Eureka is distinct from *Conchocaryon* F. Muell. 1879, which has asymmetric fruits and laterally attached winged seeds (Mueller 1879; Dettmann & Clifford 2005). Both *Plesiocapparis* F. Muell.1871 and *Celyphina* F. Muell. 1871 have indehiscent, unilocular, near-smooth fruits with branched vasculature in the mesocarp. They differ from *Eureka* in possessing large stone cell complexes (not radially oriented fibres) that cap and surround the vascular bundles in the fruit wall (Dettmann & Clifford, in prep.).

FIGS 2-16. *Eureka welcomensis* sp. nov.; **2-4**, Lateral, apical and basal views of holotype with seed (arrowed), QMF51143; scale bar = 5 mm; **5-6**, Pericarp, lateral view showing surface of locule and external lateral view showing V-shaped scar (arrowed) of style base, AMF11099; scale bar = 5 mm; **7, 8**, Pericarp, surfaces of locule, lateral view, QMF51144; scale bar =5mm; **9**, Detail of style scar (arrowed) on external surface of fruit, QMF51145; scale bar = 2.5 mm; **10**, Pericarp wall, transverse section at right angles to the dorso-ventral plane showing vasculature associated with style base (arrow), QMF51145; scale bar = 1 mm; **11, 12**, Pericarp wall, section in plane of dorsal hinge line and ventral suture showing vasculature comprising eroded vertical (v) bundles is cross section and radially aligned secondary bundles (r) surrounded by fibre complexes embedded in a ground mass of parenchyma, QMF51145; scale bar = 1 mm; **13, 14**, Pericarp wall, structure in transverse sections showing wall fibre bundle complexes surrounding vasculature, QMF51149; scale bar = 100 μm; **15, 16**, Pericarp wall in transverse section showing fibre bundles surrounding branched vasculature and detail of fibres, QMF51150; scale bar = 100 μm and 10 μm respectively.

Species - *Eureka welcomensis* sp. nov.
(Figs 2-24)

Holotype. QMF51143 (Figs 2-4). Prolate ellipsoidal, unilocular, 2-valved fruit, partially dehisced into 2 subequal valves along ventral suture and dorsal hinge line; stalk scar indistinct, scar of style base oriented transverse to dorso-ventral plane extending 4-5 mm from apex towards base on mid face of each valve. Pericarp 4-5 mm thick in lateral regions, thinner (3 mm) at apex. Seed solitary, apically attached, orthotropous. Vertical axis 19mm; lateral axes 19 mm, 16 mm.

Other material. QMF51144-QMF51151 inclusive, AMF11099.

Type locality. Herberts on Welcome Creek Drain, N of Bundaberg, Queensland; Early Miocene.

Diagnosis. Fruit woody, prolate ellipsoidal, near symmetrical about the vertical axis; indehiscent or tardily dehiscent, unilocular, with 1 apically attached seed. Stalk attachment basal, inconspicuous; style base represented by a linear groove oriented transverse to the dorso-ventral plane and extending 4-5 mm from apex on lateral surface of each valve; groove underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp with near smooth outer surface, thickest (4-6 mm) in basal and mid regions of lateral surfaces, tapering to 3-4 mm at apex and along both ventral suture and dorsal hinge line; wall comprises thin exocarp overlying a thick vascularised mesocarp and a thin cuticle-like endocarp. Inner mesocarp predominantly of vertically aligned vasculature surrounded by fibre sheaths in a ground mass of parenchyma; at or near inner/outer interface of mesocarp the vascular bundles branch radially; outer mesocarp composed of the radially directed vascular branches and surrounding fibre sheaths. Preserved seed coat comprises exotesta of a thin, structureless cuticle, an endotestal cuticle bearing impressions of polygonal-shaped transfer cells (40-60 µm diameter) having internally directed fimbriae, and a tegmic cuticle with impressions of anticlinal walls of rectilinear cells (55-70 µm long, 20-25 µm wide).

Dimensions. Pericarp (8 specimens); vertical axis 12.5 (18.5) 23 mm, lateral axes 12.5 (16.8) 22 mm (in plane of dehiscence) x 10 (15.6) 20 mm (at right angles to dorso-ventral plane). Seed (4 specimens); vertical axis 12-16 mm, lateral axis 8-10 mm.

Derivation of name. With reference to the type locality and in allusion to 'The Welcome' gold nugget, recovered during 1858, from a Deep Lead at Bakery Hill near Ballarat, Victoria.

Remarks. The majority of specimens were collected in an undehisced state (Figs 2-4), but on drying after collection, the valves of several of them separated either partially or wholly from the apex and along the ventral suture thereby to reveal their seed coats attached to the pericarp wall (Fig. 17).

Distribution. Herberts on Welcome Creek Drain, N of Bundaberg; near Clifton, Darling Downs; Picardy Station near Moranbah Hole RDPD98MA21, 123-133 m, Qld; Forest Reef, near Orange, NSW.

Age range. Early Oligocene-early Late Miocene.

Species - *Eureka turgida* (F. Muell.)
#### comb. nov. (Figs 25-30)

1874a *Conchotheca turgida* Mueller, p.42; Pl.X, 8, 12 (non figs 5-7, 9-11)

Lectotype. NMVP53987; Mueller, 1874a, Pl. X, fig. 8; Figs 25-30 herein. One valve of globose unilocular fruit, 12 mm long, 11 mm wide (dorsiventrally), stalk inserted into basal depression. Pericarp wall 2-3 mm thick; seed attached apically, with remnants of seed coat loosely adherent to pericarp in basal half of locule.

Type locality. Nintingbool, (Crucible Co.Shaft, ~23.2 m) near Haddon, SW of Ballarat, Victoria; basal sediments of a sequence beneath basalt: Oligocene-Miocene.

Diagnosis. Fruit woody, indehiscent or tardily dehiscent, spheroidal, unilocular, with 1 seed. Stalk 2-2.5 mm in diameter, inserted into basal depression 4-5 mm in diameter; style base
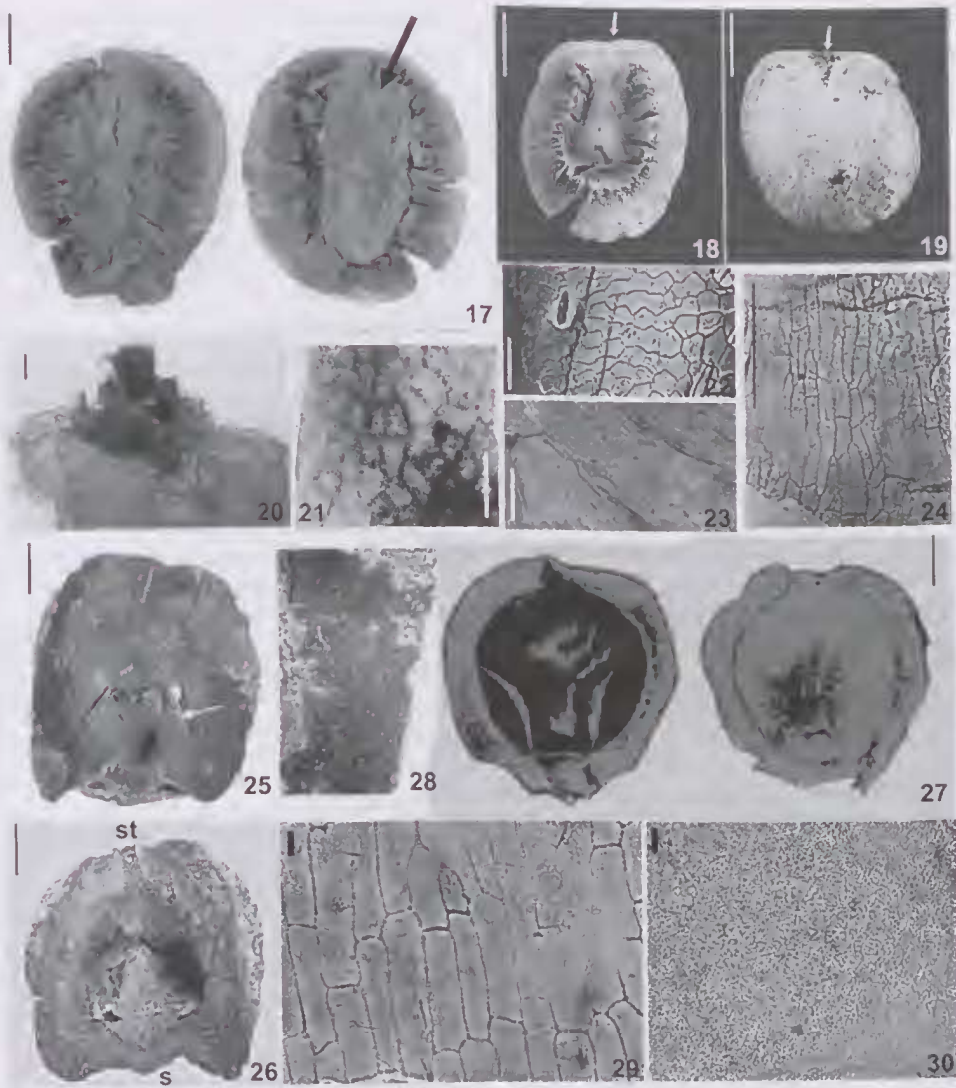
FIGS 17-30. *Eureka welcomensis* sp. nov. and *Eureka turgida* (F. Muell.) comb. nov.; **17-24,** *Eureka welcomensis* sp. nov.; **17,** Interior surfaces of opened fruit with preserved seed (arrowed), QMF51148; scale bar = 5 mm; **18, 19,** Internal and external surface, showing style base (arrowed), of one valve of opened fruit QMF51147; scale; bar = 5 mm; **20,** Cuticle of funicle and seed coat at base of seed, QMF51150; scale bar = 100 μm; **21, 22,** Inner layer of seed coat as viewed under light and scanning electron microscopes, cuticle showing impressions of polygonal-shaped transfer cells, QMF51150; scale bar = 100 μm; **23, 24,** Outer layer of seed coat as viewed under light and scanning electron microscopes, cuticle showing elongate cells, QMF51150; scale bar = 100 μm; **25-26,** *Eureka turgida* (F. Muell.) comb. nov., lectotype, interior surfaces of opened fruit showing traces to stalk (s) and stigma (st) and remnants of seed coat (arrow), NMVP53987; scale bar = 2.5 mm; **27,** Lectotype as illustrated by Mueller, NMVP53987; scale bar =2.5 mm; **28,** Detail of pericarp wall NMVP53987; scale bar = 1 mm; **29, 30,** Seed coat tissue, outer and inner layers respectively NMVP53987; scale bar = 10 μm.

represented by an ellipsoidal groove, the long axis 2-3 mm and oriented transverse to the dorso-ventral plane on lateral surface of valves; groove underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp with a near-smooth outer surface; wall 2.5-3 mm thick in mid regions of lateral surfaces, tapering to 1.5-2 mm at base of style; composed of thin exocarp overlying a thick vascularised mesocarp and a thin cuticle-like endocarp. Mesocarp a dense groundmass of fibre sheaths that surround the vasculature and are predominantly aligned in a radial direction. Preserved seed coat comprises exotesta of a thin, structureless cuticle, an endotestal cuticle bearing faint impressions of polygonal cells (40-50 μm in diameter) having occasional internally directed fimbriae, and a tegmic cuticle with impressions of anticlinal walls of rectilinear cells (80-120 μm long, 20-25 μm wide).

Dimensions. Pericarp (2 specimens); vertical axis 11, 12 mm, dorsiventral axis 10, 11 mm.

Comparison. *E. turgida* is smaller and the pericarp wall is thinner than that of *E. welcomensis*. Moreover, the latter species lacks a basal depression as occurs in *E. turgida*.

Distribution and age. Known only from the type locality: Oligocene-Miocene.

Species - *Eureka spechtii sp. nov.* (Figs 31-51)

1874a *Conchotheca turgida* Mueller, p.42; Pl.X, 5-7, 9-11 (non figs 8,12)

Holotype. (here designated) NMVP53958 (Mueller, 1874a, Pl. X , fig. 7), Figs 31-34 herein. Whole fruit, unilocular, ellipsoidal, vertical axis 13.5 mm, lateral axes each 10.5 mm. Stalk scar 3 mm.

Other material. NMVP52980, NMVP53096, NMVP53098, NMVP53960, QMF13208.

Type locality. Nintingbool, (Crucible Co.Shaft, ~23.2 m) near Haddon, SW of Ballarat, Victoria; basal sediments of a sequence beneath basalt: Oligocene-Miocene.

Diagnosis. Fruit woody, asymmetrically prolate ellipsoidal, near-smooth externally, unilocular, 1-seeded; indehiscent or tardily dehiscent, dehiscing from the apex along the sinuous, ridged ventral suture. Stalk scar indistinct or visible, 0.5-1.5 mm in diameter, inserted at base; style base indistinct, apical, underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp wall 2-2.5 mm thick in mid regions of lateral surfaces, thickening to 2.5-3.5 mm at base of style; composed of thin exocarp overlying a thick radially vascularised mesocarp and a thin cuticle-like endocarp. Mesocarp 1.8-2.2 mm in thickness in mid regions of lateral surfaces, composed of a dense groundmass of fibre sheaths that surround the vasculature and arranged predominantly in a radial direction. Preserved seed coat comprises exotesta of a thin, structureless cuticle, an endotestal cuticle bearing faint impressions of polygonal cells (40-50 μm in diameter) having occasional internally directed fimbriae, and a tegmic cuticle with impressions of anticlinal walls of rectilinear cells (80-120 μm long, 20-25 μm wide).

Dimensions. Pericarp (8 specimens); vertical axis 10 (11.8) 14 mm; lateral axes 8 (9.8) 11 mm (in plane of dehiscence) x 7.5 (8.4) 10.5 mm (at right angles to dorsal-ventral plane).

Derivation of name. Named in honour of Raymond Louis Specht, distinguished Australian ecologist.

Comparison. *E. spechtii* differs from *E. turgida* in shape (prolate ellipsoidal vs. spheroidal), wall thickness (thickest vs thinnest in apical regions) and the ventral suture line (sinuously ridged vs. straight).

Distribution. Nintingbool (Mueller, 1874a, 1874b); Foster (Deane, 1925), Victoria; Brandy Creek (Johnston 1880), Tasmania; Darling Downs (see Johnston 1880, p.27), Queensland.

Age range. Early Oligocene-early Late Miocene.

Species - *Eureka harslettiae* sp. nov.
(Figs 52-64)

Holotype (here designated).QMF51153, Figs 52-53. Whole fruit, unilocular, ellipsoidal, vertical axis 19 mm, lateral axes each 15.5 mm. Stigma scar 2.5 mm wide at apex , tapering along its length (7.5 mm) on both lateral surfaces.

Other material. QMF 51154-QMF 51157 inclusive.

Type locality. South Blackwater Coal Pty Ltd Hole R8736, 82 m, Queensland: Early-Late Oligocene.

Diagnosis. Fruit woody, indehiscent or tardily dehiscent, with a near-smooth surface; prolate ellipsoidal to subspheroidal with a prominent ridge (2-3 mm high) that encircles the stone in the longitudinal plane and situated along the ventral suture and dorsal hinge line; unilocular, 1-seeded. Stalk attachment basal, inconspicuous; style base represented by a V-shaped groove oriented perpendicular to the dorso-ventral plane and extending 7-9 mm from apex on lateral surface of each valve; groove widest (1.5-2.5 mm) at apex; underlain by vascular strands that extend into the pericarp and terminate near the seed cavity. Pericarp wall 4-6 mm thick, but thinning slightly around base of style; mostly composed of vascularised mesocarp external to a thin, cuticle-like layer (?endocarp). Mesocarp 3.8-5.8 mm in thickness, composed of a dense groundmass of fibre sheaths that surround the vascular mesh and are predominantly aligned in a radial direction. Seed coat comprises exotesta of a thin unstructured cuticle, and an endotestal cuticle bearing faint impressions of polygonal cells (40-50 µm in diameter) having sparsely distributed, internally directed fimbriae.

Derivation of name. Named in honour of Morwenna Jean Harslett, Queensland naturalist.

Dimensions. Pericarp (12 specimens); vertical axis 15 (16.7) 21 mm; lateral axes 13 (15.5) 21 mm (in plane of dehiscence) x 8 (11.8) 15 mm (at right angles to dorsal-ventral plane).

Remarks and Comparison. The holotype and all but one of the other specimens examined are charcoalified and their internal morphological and anatomical features are preserved. The sole permineralised example studied is known only from its external morphology. The species is similar in size to *E. welcomensis*, but is distinct in possessing a prominent ridge that encircles the fruit along the ventral suture and dorsal hinge line. Moreover, the V-shaped groove of the stigma scar is longer than that in *E. welcomensis*.

Distribution. South Blackwater Coal Pty Ltd Hole R8736, 82 m; Glencoe Station, near Capella, Queensland.

Age range. Early-Late Oligocene.

AFFINITIES OF *EUREKA*

Pericarp vasculature of *Eureka* is consistent with that of fruits borne by several genera of the Proteaceae included within tribe Macadamieae, and in particular by members of subtribes Macadamiinae, Gevuininae, and Virotiinae (sensu Weston and Barker, 2006; Mast et al., 2008). The pericarps of genera included within these subtribes possess a complexly branched vascular system surrounded by sclerenchyma and/or fibre sheaths and/or stone cell complexes. The main vascular bundles are predominantly vertically aligned, occurring within the middle region of the mesocarp, and external to a narrow zone of parenchyma and/or sclereids of the innermost mesocarp. The vertical bundles branch radially, the radial branches extending into the outer region of the mesocarp where they are sheathed by sclerenchyma; the tissues between them are composed of fibres, stone cell complexes and/or thin-walled (and sometimes succulent) parenchyma. Thus, the middle region of the pericarp with its vertically aligned, sheathed vasculature is densely structured and may be woody and endocarp-like, whereas the outer region of the pericarp is predominantly radially structured (Figs 65-68,
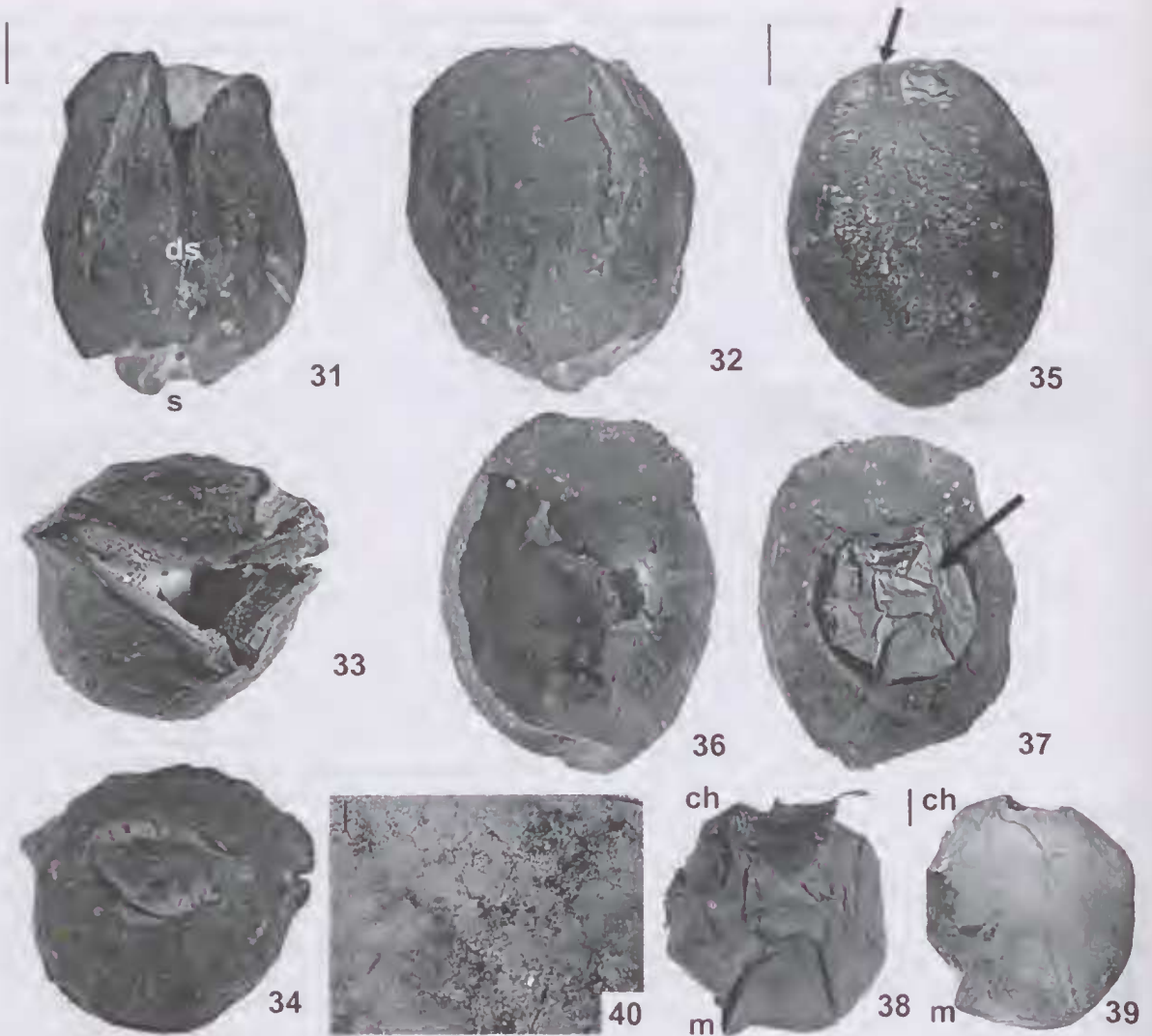
FIGS 31–41. *Eureka spechtii* sp. nov. **31-34**, Holotype in lateral (31, 32), apical (33), and basal (34) views showing dorsal suture (ds) and stalk scar (s), NMVP53598; scale bar = 2.5 mm; **35-37**, External (35) and internal (36,37) views of pericarp showing style base (arrowed) and apically attached seed (arrow), NMVP53096; scale bar = 2.5 mm; **38-39**, Seed illustrated in Fig. 37 before (38) and after (39) treatment with sodium hypochlorite showing positions of chalaza (ch) and micropyle (m), NMVP53096; scale bar = 1 mm; **40**, Transfer cells of seed coat of holotype, NMVP53598; scale bar = 10 µm.
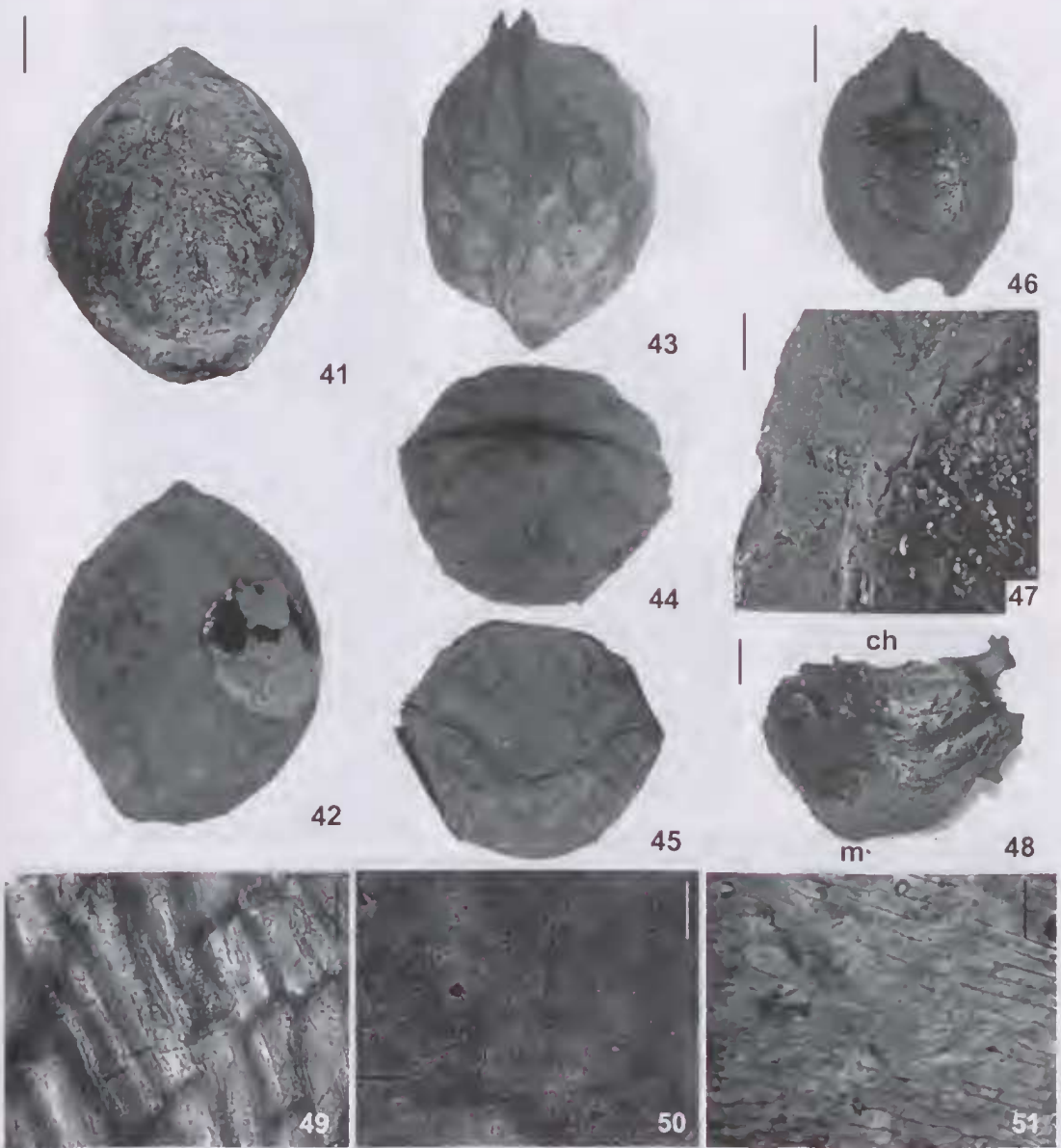
FIGS 41-51. *Eureka spechtii* sp. nov. **41-45.** Lateral (41-43), apical (44) and basal (45) views of pericarp, NMVP53960; scale bar = 2.5mm. **46-47.** Internal views of pericarp, NMVP53098; scale bars = 2.5 mm and 0.5mm respectively. **48.** Seed morphology showing chalaza (ch) and micropyle (m), NMVP53098; scale bar = 1 mm. **49.** Locule tissue, NMVP53598; scale bar = 40 μm. **50, 51.** Anatomy of seed coat showing transfer cells (50) and inner cuticle of elongate cells (51), NMVP53598; scale bars = 40μm.
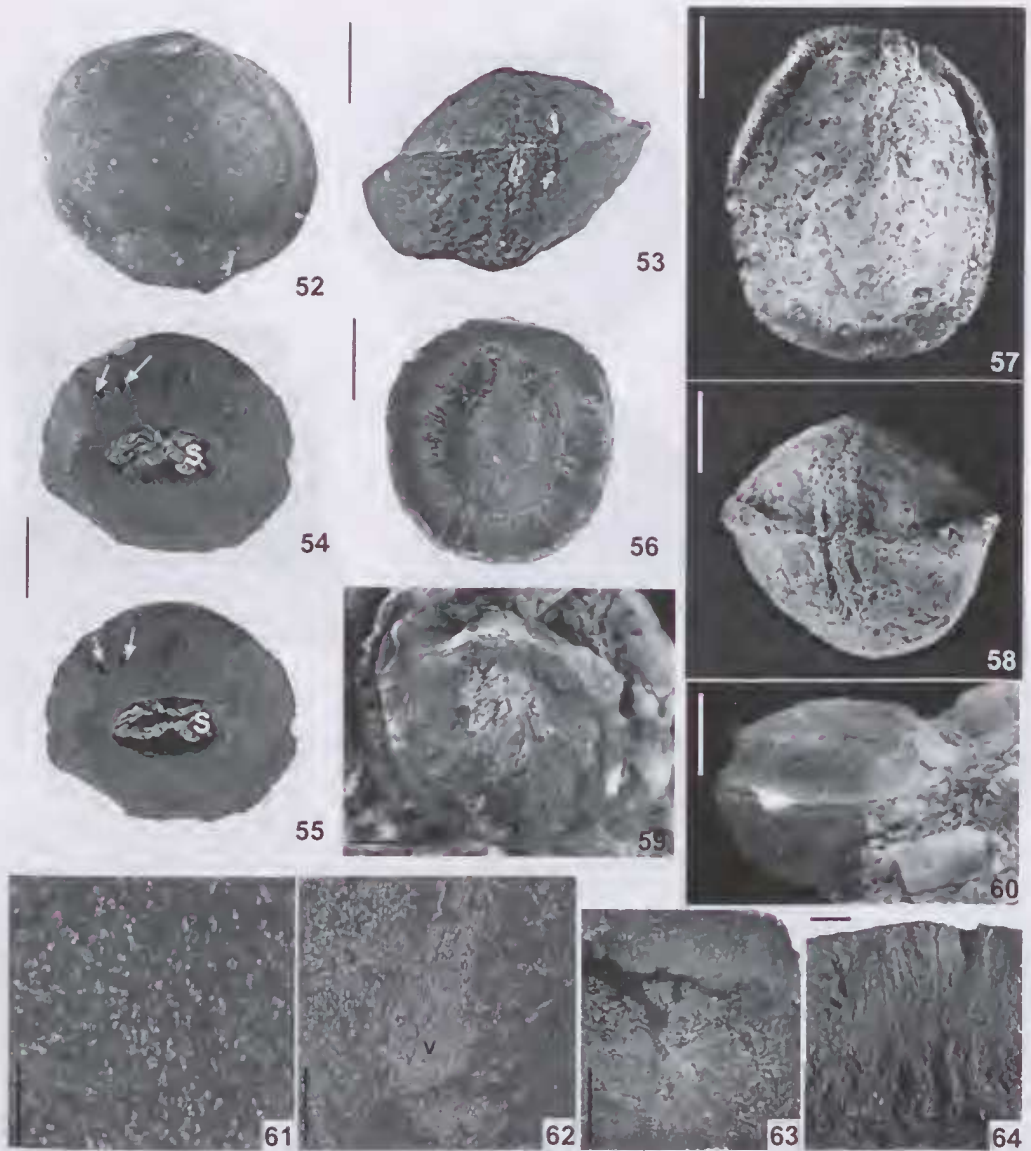
FIGS 52-64. *Eureka harslettiae* sp. nov.; **52, 53,** Holotype, lateral (52) and apical (53) views, QMF51153; scale bar = 5 mm; **54, 55,** Internal views of fruit cut transversely, showing seed (S) in locule and cavities (arrows) from which vascular bundles have been eroded from pericarp, QMF51154; scale bar = 5 mm; **56,** Internal view of pericarp cut longitudinally, QMF51155; scale bar = 5 mm; **57, 58,** Lateral and apical views, QMF51156; scale bar = 5 mm; **59, 60,** Lateral and apical views of permineralised specimen, QMF51157; scale bar = 5 mm; **61-63,** Longitudinal sections of pericarp showing vascular tissue (v) surrounded by fibre bundle complexes, QMF51155; scale bars = (100 μm, 0.5 mm, 1 mm respectively); **64,** Longitudinal section of pericarp showing radial orientation of fibre complexes surrounding partially eroded vascular bundles of the inner mesocarp region, QMF51155; scale bar = 1 mm.

TABLE 1. Fruit and seed wall characters of members of Subtribes Macadamiinae and Gevuininae (sensu Weston & Barker 2006), and fossil *Eureka*. Information sources, additional to present observations, on development and/or anatomy are from Filla (1926), Francis (1928), Hartung & Storey (1939), Hohman (1978), and Strohschen (1986a,b).

Subtribe/ fossil taxon	Fruit type/ dehiscence	Pericarp				Seed coat		
		Exocarp	Outer mesocarp	Middle mesocarp	Inner mesocarp	oe., outer integument	ie., outer integument	Seed sheath
Macadamiinae	follicle or drupaceous follicle; ?delayed dehiscence	epidermal cells with stomata and trichomes	leathery, radial vasc. and fibres	leathery vert. vasc.; outer surface smooth	parenchyma	woody or ?thin cuticle (*Panopsis*)	crystal layer, polygonal cells	thin, fragile 1-layered (derived from inner integument)
Gevuininae (excluding *Cardwellia*)	drupaceous/ follicle; delayed dehiscence	epidermal cells with stomata and trichomes	succulent-fibrous, radial vasc. and fibres	woody, vert. vasc.; outer surface smooth	parenchyma and sclereids adherent to testa	thin cuticle	crystal layer, polygonal cells	1-layered with elongate cells (derived from cuticle between outer and inner integuments)
Eureka	drupaceous/ follicle; delayed dehiscence	not known	?succulent, radial vasc. and fibres	woody, vert. vasc.; outer surface smooth	parenchyma and sclereids adherent to testa	thin cuticle	crystal layer, polygonal cells	1-layered with elongate cells

73-77, 80A-B). This pattern of vasculature was detailed for *Macadamia*, *Brabejum*, *Hicksbeachia*, and *Gevuina* by Filla (1926) and designated as fruit Type VI among the pericarps of Proteaceae known to him. Later, the vasculature pattern of pericarps was identified as a characteristic attribute (Johnson & Briggs 1973; Douglas 1995) of genera now included within subtribes Macadamiinae, Gevuininae, and Virotiinae (sensu Weston & Barker 2006).

Within these subtribes, fruits with a vascularised, radially structured pericarp and bearing 1-2, vertically attached, wingless seeds as occurs in *Eureka*, are borne by *Macadamia* F. Muell., *Panopsis* Salisb., *Brabejum* L. and *Lasjia* P.H. Weston & A.R. Mast (subtribe Macadamiinae); *Heliciopsis* Sleumer, *Athertonia* L.A.S. Johnson & B.G. Briggs, and *Virotia* L.A.S. Johnson & B.G. Briggs (subtribe Virotiinae); and *Sleumerodendon* Virot, *Euplassa* Salisb., *Gevuina* Molina, *Bleasdalea* F. Muell., *Hicksbeachia* F. Muell., *Kermadecia* Brongn. & Gris., and *Turrillia* A.C.Sm. (subtribe Gevuininae)

(Sleumer 1955; Virot 1968; Johnson & Briggs 1975; Smith & Haas 1975; Smith 1985; Steyermark 2004; Weston & Barker 2006; Mast et al. 2008). The vascularised tissues of fruits of the extant genera are of mesocarp origin as confirmed from detailed developmental studies (Francis 1928; Hartung & Storey 1939; Strohschen 1986a, b) of fruits of *Macadamia ternifolia* F. Muell., *M. integrifolia* Maiden & Betche (Subtribe Macadamiinae), and *Hicksbeachia pinnatifolia* F. Muell. (Subtribe Gevuiinae). Furthermore, an endocarp *s.str.* (ie. a proliferation of woody tissue derived from the inner epidermis of the ovary wall) is not formed in mature fruit of the studied taxa. It seems likely that the woody or sometimes leathery 'endocarp' referred to by some authors (e.g. Sleumer 1955; Virot 1968; Smith & Haas 1975) in morphological descriptions of fruits of the extant taxa within subtribes Virotiinae, Gevuininae, and Macadamiinae instead represents tissues of the mesocarp.
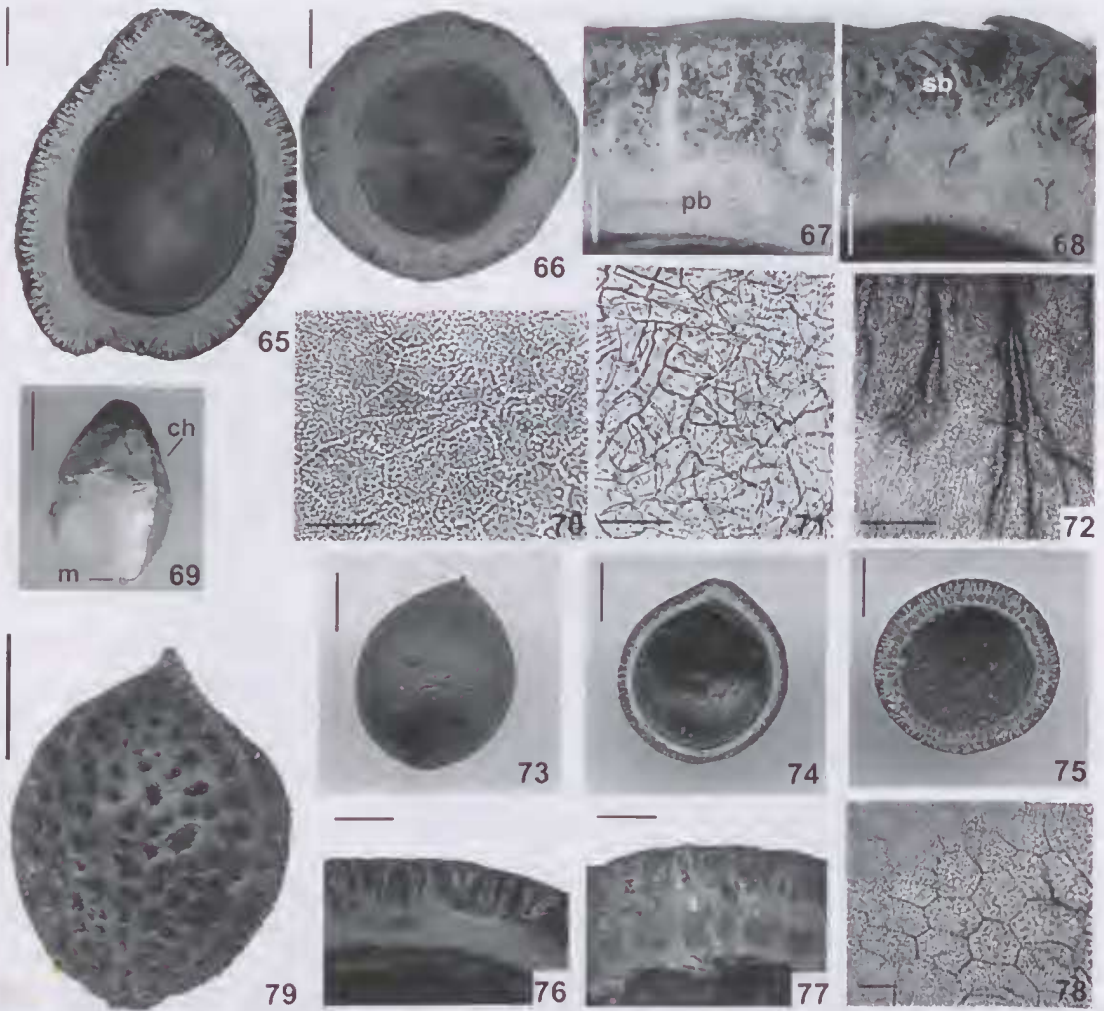
FIGS 65-79. Fruits and seeds of *Hicksbeachia pinnatifolia* F. Muell. (65-72) and *Gevuina avellana* Molina (73-78), and fruit of *Athertonia diversifolia* (C.T. White) L.A.S. Johnson & B.G. Briggs (79); 65-68, Pericarp *Hicksbeachia pinnatifolia*, longitudinal (65, 67) and transverse (66, 68) sections of pericarp showing vasculature comprising vertically aligned primary bundles (pb) of inner mesocarp and radially aligned secondary bundles (sb) extending into the exocarp; scale bars 65, 66 = 10 mm, 67 = 1 mm; 69, Seed *H. pinnatifolia*, showing chalaza (ch) and micropyle (m); scale bar = 10 mm. 70-72. Tissues associated with seeds of *H. pinnatifolia*; 70, Inner epidermis of testa showing polygonal cells with internally directed fimbriae (crystal layer); scale bar = 50 µm; 71, Endocarp sclereids detached from pericarp and closely adherent to testa; scale bar = 100 µm; 72, Chalazal tissue showing vasculature; scale bar = 0.5 mm; 73-77, Pericarp of *Gevuina avellana*, lateral view (73), longitudinal (74, 76), and transverse (75, 77) sections; scale bar = 73-75 = 5 mm, 76, 77 = 1 mm; 78,Seed tissue *G. avellana*, inner epidermis of testa showing polygonal cells with internally directed fimbriae (crystal cells); scale bar = 50 µm; 79, *Athertonia diversifolia*, pericarp with exocarp removed, lateral view showing surface reticulation of mesocarp; scale bar = 5 mm.
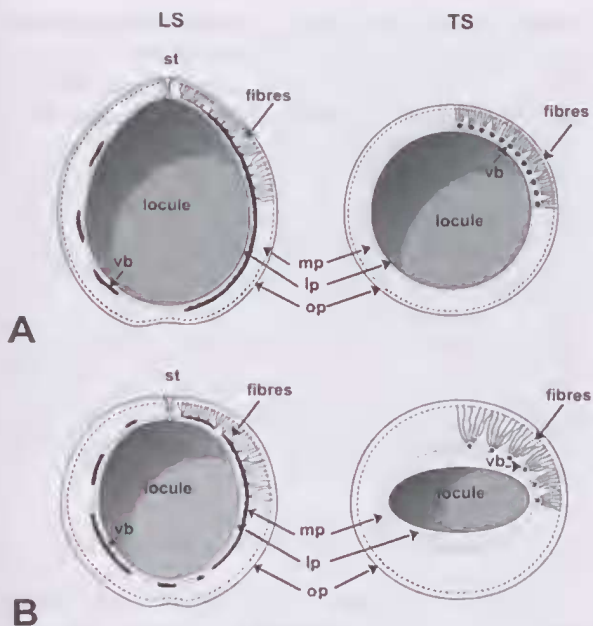
FIG. 80. Diagram illustrating pericarps of A, *Hicksbeachia pinnatifolia* and; B, *Eureka welcomensis* in longitudinal (LS) and transverse (TS) sections. ip, inner pericarp; mp, middle pericarp; op, outer pericarp; st, stigma scar; vb, vascular bundles.

Fruits of several genera within the Macadamiinae (*Macadamia, Nothorites,* and *Lasji*) are characterised as follicular (Willis 2007; Mast et al. 2008) as demonstrated from developmental studies of *Macadamia* (Francis 1928; Hartung & Storey 1939; Strohschen 1986a). The fruits dehisce along the entire or partial length of the ventral suture of the mature pericarp. Fruits of the other extant Macadamiinae (*Brabejum* and *Panopsis*) are characterised as indehiscent to tardily indehiscent (Willis 2007; Mast et al. 2008). However, by contrast to the woody pericarp of *Eureka*, the pericarp of *Brabejum* lacks significant lignified tissue (Filla 1926), whereas detailed anatomical and developmental studies have yet to be undertaken on fruits of *Panopsis* (Edwards & Prance 1993).

Developmental studies confirm that the indehiscent to tardily dehiscent pericarps of *Hicksbeachia*

pinnatifolia are transitional between a follicle and a nut (Strohschen, 1986b). Fruits of this and other taxa included in subtribe Gevuininae (except *Cardwellia*) and those of subtribe Virotiinae are described as 'drupaceous', in possessing a woody, vascularised middle mesocarp and an outer, somewhat fleshy mesocarp with radially orientated vascular and fibre bundles (Weston & Barker 2006, p. 338; Mast et al. 2008). In fruits of the Virotiinae, the woody middle mesocarp possesses a reticulate or pitted outer surface (Sleumer 1955; Rozefelds 1990, 1992; Fig. 79) whereas, except for *Sleumerodendron austrocaledonicum*, the middle mesocarp of indehiscent fruits of the Gevuininae has a smooth surface (Figs. 73, 80A). The surface of the woody middle mesocarp of *S. austrocaledonicum* is sculpted into a series of irregular branched longitudinally-aligned, ribbon-like strips that are separated by transversely disposed fibres (Association Endémia 2001).

Thus the smooth-surfaced, vascularised, radially structured pericarps of *Eureka* are more similar in morphology to the indehiscent/tardily dehiscent fruits of *Panopsis* (Macadamiinae) and the Gevuininae than to those of the Virotiinae and Malagasiinae, each of which has a well defined synapomorphy. In the Virotiinae the inner mesocarp surface is pitted or reticulate, and in the Malagasiinae the outer mesocarp lacks prominent radiating vascular bundles (Weston & Barker 2006). Moreover, in Macadamiinae seeds possess a structureless, fragile seed sheath derived from the inner integument, whereas in studied seeds of the Gevuininae the seed sheath is a cuticle with elongate cells derived from a cuticle between the inner and outer integument (Table 1). Seeds of *Eureka* have an inner seed layer morphologically comparable to that of *Bleasdalea, Gevuina* and *Hicksbeachia* As the phylogeny of the character states displayed by *Eureka* has not been explored, it is uncertain whether they are synapomorphic of the Gevuininae; this matter is the subject of ongoing research.

Fruits of *Eureka* are prolate ellipsoidal, near symmetrical about the vertical axis, with the stalk and style in vertical alignment and the dorsal hinge line and ventral suture near equal in length. Extant Gevuininae having fruits possessing these features are *Gevuina, Hicksbeachia, Bleasdalea, Euplassa*, and *Turrillia*. Indehiscent or tardily dehiscent fruits of other genera comprising Subtribe Gevuininae differ in being asymmetric with respect to the vertical axis (*Sleumerodendron* – see Smith & Haas 1975) or in possessing an angled inner mesocarp (*Kermadecia* - see Smith & Haas 1975). *Eureka* possesses a single, wingless, orthotropous seed with a two layered seed coat, characters that are in accord with those detailed for *Gevuina* and *Hicksbeachia* (Hohmann 1978; Strohschen 1986b) and observed by us in these two genera and in *Bleasdalea* (Figs 70-72, 78). In each of the fossil species, the outer layer of the seed coat is closely adherent to the inner surface of the pericarp (Figs 65, 74) and envelops a cuticle bearing impressions of polygonal cells having internally directed fimbriae; these layers are interpreted to represent the outer and inner epidermis of the testa as has been precisely detailed for *Gevuina* and *Hicksbeachia* (Hohmann 1978; Strohschen 1986b). Strohschen's developmental studies confirm that in *Hicksbeachia pinnatifolia* F. Muell. tissues of the ovary wall and the outer layer (outer epidermis of outer integument) of the seed coat may be fused as is evident in *Gevuina avellana* Moliner (Hohmann 1978) and in *Eureka welcomensis*. Moreover, in both extant taxa (and in most grevilleoid genera) the inner epidermis of the testa is composed of polygonal-shaped, calcium oxalate-bearing, transfer cells with internally directed fimbriae (Hohman 1978; Strohschen 1986b). A further cuticle with impressions of elongate cells occurs beneath the testa and develops from the cuticles between the inner and outer integuments and the cuticle surrounding the nucellus (Strohschen 1986b); a morpho-logically comparable cuticle occurs beneath the testal cuticles in *Eureka welcomensis, E. turgida*,

and *E. spechtii* (Figs 23, 24, 29, 51). Anatomical and morphological features of fruits of extant species of *Turrillia* and *Euplassa* (Gevuininae) and *Panopsis* (Macadamiinae) are unavailable and so detailed comparisons between these extant fruits and fossil *Eureka* are precluded.

In summation, fossil fruits included within *Eureka* have pericarps that possess a mosaic of morphological, anatomical, and organisational attributes consistent with pericarps of the Macadamiinae and Gevuinineae. However, seed coat structure of *Eureka* is more similar to that of the Gevuininae than the Macadamiinae (Table 1) and so the fossil taxon is provisionally placed in the Gevuininae.

IMPLICATIONS OF *EUREKA*

The fossils herein allocated to *Eureka* collectively imply a wide distribution of their parental plants in eastern Australia during Oligocene and Miocene times. Oldest occurrences are in sediments beneath basalts dated as 27-34 Mya (Oligocene) in central Queensland (Picardy, Blackwater) and youngest well-dated occurrences are also in sediments beneath basalts of 11.2-13 Mya (late Middle-early Late Miocene) at Forest Reefs Mine, New South Wales. Other localities from which *Eureka* has been reported are less precisely dated, but are within an Oligocene-Miocene age frame (34-5 Mya). If *Eureka* is a member of Gevuininae, this age range has implications for the history and past distribution of subtribe and for age calibrations relevant to divergence of those taxa of the subtribe having tardily dehiscent fruits with wingless seeds. Extant members of the subtribe that bear tardily dehiscent fruits with 1-2 wingless seeds are *Hicksbeachia* and *Bleasdalea* in northeastern Australia-New Guinea, *Kermadecia* and *Sleumerodendron* in New Caledonia, *Turrillia* in Fiji and Vanuatu, and *Euplassa* and *Gevuina* in South America (Weston & Barker 2006). *Euplassa* with 20 species has the widest distribution

range (mid-low latitudes of South America) whilst each of the other six genera has a narrow distribution range and few species (Fig. 1). Initially allocated to three separate subtribes within tribe Macadamieae (Johnson & Briggs 1975) molecular and morphological analyses (Hoot & Douglas 1998; Weston & Barker 2006) demonstrated the above-named genera together with *Cardwellia* (follicular fruit with winged seeds) form a monophyletic clade. The biogeography of the clade was investigated subsequently to test whether the present trans-southern Pacific distribution of the subtribe is better explained by vicariance or by transoceanic dispersal (Barker et al. 2007; Mast et al. 2008; Sauquet et al. 2009).

Age estimates based on Bayesian phylo-genetic and molecular dating together with fossil calibration points returned an age of 51.4 (±10.5) Mya for divergence of subtribe Gevuininae (Barker et al. 2007, Fig.2, Node F), an age consistent with a vicariance model for its present distribution. By contrast, in their analyses of a more refined phylogeny of tribe Macadamieae (Mast et al. 2008) the minimum age for the most recent common ancestor (MRCA) of subtribe Gevuininae was set at 34 Mya based on the age of fossil cuticles assigned to the Gevuininae and reported from Middle Eocene sediments (Carpenter & Pole 1995). Even so, Mast et al. (2008) considered the analyses failed to discriminate between disjunction of the subtribe at 34 Mya or 13.6 Mya, and hence between a vicariance or dispersal model to account for the extant distribution of the genera in the Gevuininae. However, they propose an inferred age of 11.5 Mya for divergence between *Bleasdalea* (New Guinea and Australia) and its sister *Hicksbeachia* (Australia), and 8.1 Mya for disjunction between the sister taxa *Kermadecia* (New Caledonia) and *Turrillia* (Fiji and Vanuatu). Accordingly, they argue that long distance dispersal accounts for the distribution of the latter sister taxa since the inferred age of disjunction postdates the tectonic events that account for

the present day geography of this part of the southwest Pacific (Schellart et al. 2006). They propose that tardily dehiscent fruits with a spongy pericarp may be sufficiently buoyant for long distance water dispersal and suggest the Antarctic Circumpolar Current (ACC) may serve as a possible mechanism. This current is now believed to have been initiated in the Late Oligocene at 25-23 Mya (Lyle et al. 2009), and is confined to latitudes of approximately 40°S.

A further analysis based entirely on molecular data (Sauquet et al. 2009) yielded a cladogram whose topology for the subtribe differed from that presented by Mast et al. (2008), and different crown group age estimates for the constituent extant members of the clade. The age constraint of 70.7 Mya selected for the MRCA of crown Macadamiaeae (Sauquet et al. 2009; Fig. 1, Node I) is based on the Late Cretaceous occurrence of the fossil pollen taxon *Propylipollis crotonioides* Dettmann & Jarzen, which in parsimony analyses was considered suitable for calibration (Sauquet et al. 2009, Supporting Information, Fig. S2, Table S1). On this basis, the crown group age of Gevuininae was estimated as 37.4 Mya and 19.2 Mya for the crown group age of the clade sister to *Cardwellia* (comprising *Bleasdalea* and its sister taxa, all of which bear tardily dehiscent fruits). As discussed above the fruits of *Eureka* closely resemble those of *Bleasdalea*, *Gevuina* and *Hicksbeachia* and so the occurrence of *Eureka* in sediments as old as, or older than, 34 Mya (ie Early Oligocene) suggests that the crown group age of the sister clade to *Cardwellia*, proposed by Sauquet et al. (2009), may need to be reconsidered.

Based on occurrences of *Eureka* reported herein, the Oligocene-Miocene distribution of members of the subtribe having tardily dehiscent fruits spanned some 20° of latitude (~60°– 40°S palaeolatitude) in eastern Australia (Fig 1B). Other fossils reported from within this latitudinal band and accepted as those of the Gevuininae (Mast et al. 2008) are cuticles from the Middle

Eocene of southern Western Australia (Carpenter & Pole 1995) and the Early Miocene of New Zealand (Pole 1998). Thus, the fossil evidence demonstrates a former trans-Tasman distribution of the Gevuininae no longer mirrored in the present vegetation.

Questionably allied to the subtribe is fossil wood reported as similar to, but not identical with, that of *Gevuina* from the Oligocene of southern South America (Pujana, 2007). The pollen taxon, *Propylipollis reticuloscabratus* (Harris) Martin & Harris, which is widely distributed in Australian Campanian-Pleistocene sediments and known also from the Campanian-Eocene of the Antarctic Peninsula (Dettmann & Jarzen 1996), may not represent evidence of the subtribe in South America, as has been determined by Sauquet et al. (2009, Supporting Information). Though these authors undertook a cladistical analysis embracing pollen of all extant genera of Proteaceae and 25 fossil proteaceous-like pollen taxa, the results must be treated with caution because of the 22 pollen characters scored for pollen of extant species relatively few were available for most fossil taxa.

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